

THE GERBERA COMPLEX (ASTERACEAE: MUTISIEAE): TO SPLIT OR NOT TO SPLIT

Liliana Katinas

Departamento Científico de Plantas Vasculares
Museo de La Plata
Paseo del Bosque
1900 La Plata, ARGENTINA

ABSTRACT

The transfer of *Chaptalia hintonii* to the genus *Gerbera* was rejected by Nesom (this issue), who retains the species in *Chaptalia* sect. *Chaptalia*. *Chaptalia* and *Gerbera* belong to the *Gerbera*-complex, a group of scapose genera whose circumscriptions are still in flux and whose largest genera still lack complete revisions. Important morphological characters of the corollas, staminodes, and cypselas are discussed, and a key to genera of the *Gerbera*-complex is provided. The short, filiform corollas of the inner ray florets and the lack of staminodes are characters that allow the circumscription of *Chaptalia*. Certain species must be excluded from this genus and the sections within it must be redefined. Staminodes and inner ray florets with bilabiate corollas that are longer than the style are two characters that confirm the transfer of *Chaptalia hintonii* into the genus *Gerbera*.

KEY WORDS: *Gerbera hintonii*, *Chaptalia*, *Gerbera*-complex, corollas, staminodes, cypselas hairs

RESUMEN

La transferencia de *Chaptalia hintonii* al género *Gerbera* fue rechazada por Nesom (este volumen), quien retiene esta especie en *Chaptalia* sect. *Chaptalia*. *Chaptalia* y *Gerbera* pertenecen al complejo *Gerbera*, un grupo de géneros de hábito herbáceo escaposo, cuya circunscripción no está definida y cuyos géneros más numerosos aún carecen de revisiones taxonómicas. Se discuten los caracteres morfológicos más importantes de corola, estaminodios y pelos de la cipsela, y se provee una clave de los géneros del complejo *Gerbera*. Las corolas cortas y filiformes de las flores más internas del radio y la ausencia de estaminodios son caracteres que permiten la circunscripción de *Chaptalia*. Ciertas especies deben ser excluidas de *Chaptalia*, y las secciones de este género deben ser redefinidas. La presencia de estaminodios y de flores internas del radio con corola bilabiada más larga que el estilo constituyen dos caracteres que confirman la transferencia de *Chaptalia hintonii* al género *Gerbera*.

In a recent paper (this issue), Nesom rejected Katinas' (1998) placement of the south-central Mexican species *Chaptalia hintonii* Bullock (Asteraceae, Mutisieae) in the Old World genus *Gerbera*. He argued that no clear position within *Gerbera* was given for the species in Katinas' paper and that the morphological evidence more strongly supports including *C. hintonii* within *Chaptalia* rather than in *Gerbera*. *Chaptalia* and *Gerbera* belong to the *Gerbera*-complex, a group of seven genera whose limits are as yet in flux.

I agree with Nesom's argument that a taxonomic decision should be made in a broad context. Therefore, I take this opportunity to clarify and extend my earlier remarks on *Gerbera hintonii* (Bullock) Katinas considering here the entire *Gerbera*-complex.

A revision of the genus *Chaptalia* in progress, led me to examine all the species of this taxon and many of the species of the other genera of the *Gerbera*-complex. This broad perspective allowed me to determine the potential key characters that can be used to circumscribe the genera of the complex. Furthermore, I found ca. 15 species included in *Chaptalia* that are best excluded from this genus (Katinas, in prep.), some of which probably are better placed within *Gerbera*. The transfer of *C. hintonii* to *Gerbera* was a first step toward this goal.

It should be remarked that since the studies on this group are not finished yet (e.g., revisions of *Chaptalia*, *Gerbera*, and *Leibnitzia*), some conclusions presented here should be regarded as provisional. The main purpose of this presentation is to provide an overview of the transfer of *Chaptalia hintonii* to *Gerbera* in the broader context of the *Gerbera*-complex.

The problem

The *Gerbera*-complex or the scapose-complex (Jeffrey 1967; Hansen 1985a, 1990) belongs to Mutisiinae (tribe Mutisieae) a predominantly American subtribe with a few genera and species occurring in Asia and Africa. The complex, with ca. 100 species characterized by monocephalous scapes, consists of the genera *Chaptalia* Vent. (ca. 35 species), *Gerbera* L. (29 species), *Leibnitzia* Cass. (six species), *Lulia* Zardini (one species), *Perdicium* L. (two species), *Trichocline* Cass. (22 species), and *Uechtrizia* Freyn (three species). Recently, Hind (2001) transferred *Trichocline spathulata*, the only Australian species of the South American genus *Trichocline*, to the genus *Amblyperma*. A re-examination of both genera however, led to return *Amblyperma* to the synonymy of *Trichocline* (Katinas 2004).

The circumscription of taxa within this morphologically homogeneous group, which lacks complete treatments for its largest genera, has been very problematic. Except for the small genera *Lulia*, *Perdicium* and *Uechtrizia*, the only complete systematic revision within the complex is for *Trichocline* (Zardini 1975). The remaining genera still need complete treatments. In the case of *Chaptalia*, Burkart (1944) focused on the Argentinian species, and Nesom (1995) treated the North and continental Central American species. In addition, Nesom (1983) revised the American species of *Leibnitzia*, whereas Hansen (1988) treated the Asiatic ones. Similarly, Hansen (1985a, b, 1988) treated separately the different sections of *Gerbera*, but he did not deal with the genus as a whole.

In all these studies, the authors stated the difficulties in circumscribing each genus due to the small differences among them. In many cases transfers were made from one genus to another, e.g., species from *Trichocline* to *Gerbera* (Zardini 1974), species from *Chaptalia* to *Leibnitzia* (Nesom 1983), species from *Chaptalia* to *Gerbera* (Katinas 1998). One caulescent species of *Trichocline* had the new genus *Lulia* (Zardini 1980) created for it (which may be excluded from the complex).

Contrasting potential solutions were proposed to deal with these conflict-

ing treatments. Some would treat the entire *Gerbera*-complex as a single, large genus (e.g., Hansen 1990), and, then again, some would split the complex into smaller genera (e.g., Jeffrey 1967). Resolution of the problem will probably only be achieved when treatments of all the taxa are completed.

What character?

Nesom referred to some morphological characters when discussing the transfer of *Chaptalia hintonii* to *Gerbera*, and arguing for the inclusion of this species in *Chaptalia* sect. *Chaptalia*. Below I discuss these characters in the context of the entire *Gerbera*-complex.

Vegetative characters allow some distinction among genera of the *Gerbera*-complex, but reproductive ones, mainly florets (number of series per capitulum, type of corollas, style branches, staminodes) and fruits (cypsela apex, cypsela hairs) seem to be more useful for the delimitation of taxa.

A part of *Gerbera*, and the genera *Lulia*, *Trichocline*, and *Uechtritizia* have their capitula biseriata (two types of florets), i.e., ray florets bilabiate and disc florets bilabiate. *Leibnitzia* also has two types of florets, with ray florets ligulate or bilabiate, sometimes with a minute inner lip (e.g., *L. occimadrensis*), and disc florets tubular or bilabiate. *Perdicium* and a part of *Gerbera* have three types of florets, all bilabiate. *Chaptalia* also has triseriate capitula, with the outer ray florets mostly ligulate and in some species (e.g., *C. exscapa*, *C. tomentosa*) an inner lip is developed. The corolla of the inner ray florets is very reduced, filiform, with a narrow tube, and irregularly bilabiate, tubular or ligulate 3-lobed, shorter than the style. This short, reduced corolla separates *Chaptalia* from *Gerbera*. I have found only two species, *C. mandonii* and *C. tomentosa*, where longer corollas of the inner ray florets may exist, but here they are generally mixed with short ones in the same capitulum. I also found in *Gerbera* some specimens (e.g., *G. piloselloides* and *G. viridifolia*) with corollas that approach those of *Chaptalia* in that their inner ray florets are reduced and transitional between the outer ray florets and the disc florets, but here they are bilabiate and as long as the style or longer. This longer, more developed corolla is present in *G. hintonii* as I have already pointed out (Katinas 1998).

A point considered by Nesom is the presence and the degree of development of staminodes in *Chaptalia* and *Gerbera*. Hansen (1990) showed that there is a reduction series in the staminodes of the ray florets from well developed staminodes or sterile anthers (*Lulia*, *Trichocline*, *Uechtritizia*, part of *Gerbera*), vestigial (part of *Gerbera*, part of *Leibnitzia*, part of *Perdicium*) to absent (*Chaptalia*). *Gerbera parva* is the only species in the genus that lacks staminodes. Observations on different specimens of *G. piloselloides* show that staminodes can be present or absent (even in the same capitulum), the same situation that occurs in *G. hintonii*. Nesom pointed out that staminodes are found in species of *Chaptalia*, e.g., *C. estribensis*, *C. hololeuca*, *C. incana*, and *C.*

texana. The first three species, which have staminodes and lack the typical inner ray floret of *Chaptalia*, are included in the group that I would exclude from the genus. With respect to *C. texana*, Nesom (1995) reports that certain specimens (Gentry & Fox 11768) have staminodes. The approximately 55 specimens of this species that I have seen all lack staminodes. Moreover, the two sheets of Gentry & Fox 11768 (MEXU, with the numbers 47607 and 132933) that I have seen lack staminodes as well. *Chaptalia texana*, in addition, is a species that has all the typical characters of *Chaptalia* (e.g., the corollas discussed above). Finally, unlike Nesom I do not consider that the vestigial staminodes, present in *G. hintonii* and other taxa, should be interpreted as a plesiomorphic similarity. As I previously pointed out (Katinas 1998: 381) the reduction of staminodes to thread like (or vestigial) structures as well as their complete absence represent apomorphic conditions.

Nesom also discusses cypselas hairs, in particular the twin hairs. According to him, the cypselas vestiture (together with nodding buds) is a synapomorphy (phylogenetic coherence) of *Chaptalia*. He also suggests that variation of the type of hairs (together with erect buds and cleistogamous heads) will allow the separation of a part of *Chaptalia* at generic rank. A complete classification of these hairs can be found in a work on Nassauviinae (Freire & Katinas 1995), the sister subtribe of Mutisiinae, and a discussion and description of the cypselas hairs in the *Gerbera*-complex is found in my previous paper (Katinas 1998: 381). The analysis of the cypselas twin hairs in most species of all genera of the complex led me to the same conclusion that Hansen (1990) came to, namely that this character is mainly useful in the distinction of *Uechtritzia*, with very long, filiform twin hairs (ca. 1 mm long). The type of twin hairs can differentiate *Chaptalia* and *Gerbera* to some degree, due to some sections of *Gerbera* having cypselas covered by filiform hairs, a type of hair that *Chaptalia* lacks. A distinction can also be made between the American *Leibnitzia* with divergent, radiate, and crenate twin hairs and the remaining genera of the *Gerbera*-complex. *Gerbera hintonii*, shares with many species of *Gerbera*, *Chaptalia* and other genera of the complex, the same type of hair (basic, rounded).

The following key delimits the genera of the *Gerbera*-complex using the characters discussed above, together with some others:

1. Caulescent herbs. Leaves parallel-nerved _____ **Lulia**
1. Acaulescent herbs. Leaves reticulate-nerved.
 2. Pappus bristles connate at the base _____ **Perdicium**
 2. Pappus bristles free.
 3. Plants dimorphic: A vernal generation with small leaves, slightly developed, and chasmogamous capitula, and an aestival generation with large leaves, fully developed, and cleistogamous capitula _____ **Leibnitzia**
 3. Plants not dimorphic.
 4. Cypselas truncate at the apex.
 5. Cypselas shaggy, covered by long hairs, ca. 1 mm long _____ **Uechtritzia**

5. Cypselas papillose, covered by short hairs, 30–50 μm _____ **Trichocline**
4. Cypselas rostrate at the apex.
6. Capitula dimorphic or trimorphic; when trimorphic, the inner ray florets with corolla bilabiate or filiform bilabiate, as long as the style or longer. Stamines generally present _____ **Gerbera**
6. Capitula trimorphic; the inner ray florets with corolla very reduced, filiform (irregularly tubular, ligulate or bilabiate), shorter than the style. Stamines absent _____ **Chaptalia**

CONCLUSIONS

As mentioned above, these conclusions are provisional, depending on the completion of work on some genera of the *Gerbera*-complex. The exclusion of ca. 15 species currently included in *Chaptalia* will be crucial for the re-definition of this genus, as many of them have characters that approach those of *Gerbera* and may eventually be transferred to that genus.

With the removal of certain species, the sections within *Chaptalia* must be redefined. The controversial *C. hintonii*, which had been put in sect. *Chaptalia*, has already been excluded (Katinas 1998). Now it is necessary to study all the species of this genus to re-evaluate the traditional sections. For instance, the characters mentioned by Nesom defining section *Chaptalia* (monocephalous, ebracteate or few-bracted scapes, heads nodding in bud, broad, cream coloured rays with a purple midstripe, and functionally staminate disc flowers) are present also in species belonging to other sections established by Burkart (1944), e.g., *C. denticulata* from Brazil (sect. *Archichaptalia*), *C. meridensis* from Venezuela (sect. *Archichaptalia*), *C. paramensis* from Colombia.

I agree with Nesom that *Chaptalia* is a natural group, although I disagree that the cypselas vestiture and nodding buds give coherence to the genus. The basic twin hairs differentiate *Chaptalia* and other taxa of the *Gerbera*-complex only to some degree, whereas nodding buds are not present in many species of *Chaptalia* (e.g., *C. dentata*, *C. exscapa*, *C. mandonii*, *C. piloselloides*, *C. runcinata*). The corolla morphology of the inner ray florets, on the other hand, seem to be the most consistent, apomorphic character for circumscribing the genus. The lack of staminodes, a condition found also (though uncommonly) in *Gerbera*, can also help to circumscribe *Chaptalia*.

In contrast, *Gerbera* has proved to be a non monophyletic genus (Hansen 1990). This situation and the potential addition of species from *Chaptalia* makes it necessary to completely revise the genus. For this reason, it is premature to consider if *Gerbera* could be split in new, small, genera. I believe that at least some genera of the *Gerbera*-complex have characters that allow them to be maintained as independent taxa within the complex, i.e., the parallel-nerved leaves of *Lulia*, the long, filiform twin hairs on the cypselas of *Uechtrizia*, the alternating plant phases of *Leibnitzia*, and the morphology of the inner ray corollas of *Chaptalia*.

Finally, I conclude that the characters exhibited by *Gerbera hintonii*, i.e., bilabiate inner ray florets with corollas surpassing the style, and vestigial staminodes provide good support for positioning it in *Gerbera* rather than in *Chaptalia*.

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